**ECOSYSTEMS**

# Tree Neighbourhood Diversity Has Negligible Effects on Drought Resilience of European Beech, Silver Fir and Norway Spruce

Loïc Gillerot,[1]* David I. Forrester,[2,3] Alessandra Bottero,[2,3] Andreas Rigling,[2,3,4] and Mathieu Lévesque[1]

[1]Forest Management Group, Institute of Terrestrial Ecosystems, ETH Zurich, Zurich, Switzerland; [2]Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland; [3]SwissForestLab, Birmensdorf, Switzerland; [4]Institute of Terrestrial Ecosystems, ETH Zurich, Zurich, Switzerland

## ABSTRACT

Promoting tree species diversity is commonly advocated in the anticipation of predicted increases in drought frequency and severity. However, mixing effects on drought responses vary substantially with site conditions and species identity. We combined annually resolved tree-ring data and repeated forest inventory data spanning the last 90 years to examine the effect of species-specific neighbourhood competition on the drought response (resistance, recovery and resilience) of European beech (*Fagus sylvatica*), silver fir (*Abies alba*) and Norway spruce (*Picea abies*) for six drought events that occurred since the 1970s at three sites in Switzerland. We found predominantly weak neighbourhood competition and tree species diversity effects, with significant interspecific influences only for resistance and recovery of beech. These minor neighbourhood effects were outweighed by tree age and size effects. Although age effects depended on species identity and components of resilience, tree size consistently negatively affected all species. Our results emphasize that diversity effects may vary for each given species combination which makes broader conclusions challenging. This is because species interact through their specific set of traits and interactions vary in space and time. Adaptive management strategies are likely to be more effective when they promote more drought-tolerant species and reductions in stand density. Despite the absence of an unequivocal advantage of tree diversity on drought resilience, striving towards species-rich forests nonetheless allows for a risk spreading among multiple species and the reinforced provision of numerous ecosystem services.

**Key words:** *Abies alba*; *Fagus sylvatica*; *Picea abies*; Species diversity; Neighbourhood competition; Mixed forest; Tree ring; Permanent plot.

## HIGHLIGHTS

- Tree size negatively impacts drought response, and age effects vary.
- Neighbourhood effects on tree drought response are weak and inconsistent.
- Species identity and local conditions likely overshadow tree diversity effects.

## INTRODUCTION

Global warming is expected to exacerbate drought frequency and severity in many regions worldwide (IPCC 2018). For Central Europe, the most recent scenarios indicate an increase in spring and summer drought frequency (Trenberth and others 2014; CH2018 2018; Spinoni and others 2018). This may have some important consequences for forest ecosystems because hotter droughts and reduced precipitation can lead to a reduction in growth (Lévesque and others 2013, 2014) that can eventually lead to mortality (Camarero and others 2015). This increased mortality was observed not only in drought-prone regions but also in mesic forests worldwide (Allen and others 2010) and is exemplified by recent die-offs in Central European Forests (Rigling and others 2018). Finding the right management strategies to make Central European forests more resilient in the face of global warming is thus crucial for sustaining the provision of ecosystem services (Gamfeldt and others 2013).

One silvicultural option of particular interest is to increase tree species diversity, the main argument is that this may reduce the overall competition for limiting resources, such as water, by a more efficient partitioning through spatial or temporal resource-use stratification (Loreau and Hector 2001; Hooper and others 2005; Forrester 2014). Some studies have found that mixed forests can sustain higher productivity levels and show increased drought resistance compared to their monospecific counterparts as a result of complementarity effects (Lebourgeois and others 2013; Pretzsch and others 2017) and, in doing so, stabilize productivity over time (Morin and others 2014; Aussenac and others 2018). The term complementarity condenses two simultaneously occurring processes: competitive reduction (that is, when intraspecific exceeds interspecific competition) and facilitation (that is, when one species improves the growth or survival of another) (Loreau and Hector 2001; Forrester 2014). Although many light-, water- and nutrient-related processes have been associated with complementarity effects (Forrester and Bauhus 2016), less is known about whether the higher resistance to extreme climatic events arises from a simple risk spreading over multiple species or whether other synergistic interactions are at play (Bauhus and others 2017).

Studies in Central European forests have yielded inconsistent results, sometimes indicating positive, neutral or even negative diversity effects on productivity and drought resistance (Forrester and Bauhus 2016; Ammer 2018; Grossiord 2018). Although evidence points towards a positive diversity effect in many forest types worldwide (Jactel and others 2018), this is not necessarily true for relatively species-poor and intensively managed forests in Central Europe. Inconsistencies often arise because of two crucial factors: (1) species identity effects and (2) the influence of local site conditions (Pretzsch and others 2017; Ammer 2018).

Species identity, as opposed to species richness, can be important because species interactions that improve water availability, water uptake or water-use efficiency (for example, possibly resulting from mixing evergreen vs. deciduous, isohydric vs. anisohydric, deep vs. shallow rooting species) can be beneficial not only for productivity in general, but also during extreme droughts (Forrester and Bauhus 2016; Gazol and Camarero 2016; Tobner and others 2016). Besides identity effects, site conditions strongly influence complementarity (Pretzsch 2013; Forrester 2014; Toïgo and others 2015; Jucker and others 2016; Ratcliffe and others 2017; Mina and others 2018). The benefit provided by a given interaction can change along gradients of resource availability, climatic conditions and stand density (Forrester 2014). For example, interactions that improve water availability may be relatively more beneficial where water is limiting (Forrester and Bauhus 2016). This holds true for not only spatial changes in growing conditions, but also temporal ones. During periods of adverse conditions, such as during extremely warm and dry years, the relative importance of positive interspecific interactions has often been found to increase (Lebourgeois and others 2013; del Río and others 2014; Aussenac and others 2018), thereby stabilizing productivity (Jucker and others 2014; del Río and others 2017). Studying trees' responses to extreme droughts is of particular interest because their direct and indirect (for example, bark beetle outbreaks) impacts will cause the largest ecological and financial losses, in contrast to gradual climate change. Yet, similar to productivity, research has reported both positive and negative diversity effects on drought responses, which generally also depend

on site conditions and species identity (Grossiord and others 2014; Forrester and others 2016; Metz and others 2016; Schäfer and others 2017; Vitali and others 2018; Vanhellemont and others 2019).

To summarize, complementarity depends on how species interact through their specific set of traits, and these interactions change spatially and temporally. Additionally, complementarity is influenced by factors like stand density, tree age and tree size (Forrester and others 2013; Ding and others 2017a; Ammer 2018). To better understand the functioning of complementarity effects, it is necessary to study interactions across a range of spatiotemporal resolutions—from fine to broad scales (Forrester 2014). The majority of empirical studies investigating mixture complementarity essentially base their findings on repeated forest inventories (Condés and others 2018; Gamfeldt and others 2013; Pretzsch and others 2013a; Toïgo and others 2015; Vilà and others 2013). These allow for broadscale comparisons at the stand level, but ignore what happens during the multiannual gaps between consecutive inventories (Biondi 1999; Rohner and others 2016) and even average out the important influence of extreme periods. Investigations of complementarity based on the immediate neighbourhood of individual trees (Chamagne and others 2017; Fichtner and others 2017; Vitali and others 2018) allows the disentangling of effects of neighbourhood density, diversity and species identity if sufficient variation in these factors is included (Forrester and Bauhus 2016). Furthermore, neighbourhood analysis (that is, characterizing tree neighbourhood in terms of tree species diversity and competition) allows for the comparison of multiple species along different site conditions and the inclusion of their mixture proportion (Chamagne and others 2017; Vitali and others 2018), which would be nearly impossible by extending the often used and stand-level 'triplet design' to more than two species (for example, Pretzsch and others 2015; Thurm and others 2016; Bello and others 2019; Jourdan and others 2019). Complementarity changes over time at different temporal scales can be assessed using a combination of neighbourhood measures in repeated forest inventory and tree-ring data. Repeated forest inventory data represent the complementarity effects accumulated between two inventories and thus a multiannual or ''static'' image. A more ''dynamic'' understanding of the complementarity effects can be reached using tree rings, because they reflect the influence of climate variables at an annual variability, which is closer to the resolution at which extreme events occur (Biondi 1999; del

Río and others 2014; Rohner and others 2016). Annually resolved tree-ring data are thus particularly helpful to detect shifts in complementarity effects and identify their drivers.

Although repeated inventory data do not offer the annual resolution of tree-ring data and thus dilute the effect of extreme droughts, they have the advantage of incorporating information at the tree and stand level and usually have a very large spatial coverage (Biondi 1999; Evans and others 2017). A common limitation of dendroecological studies is that the species composition and density around a target tree at the time of sampling may not be representative of its competitive environment over time. Because of the unknown neighbourhood during droughts events that occurred many decades ago, most studies restrict their analysis to the most recent extreme drought(s) (for example, the year 2003 in Vitali and others 2018). However, by using repeated forest inventory data, this neighbourhood can be recreated over time (Weber and others 2008) and therefore enable an accurate depiction of species mixing effects over larger temporal scales.

Here, we combined tree-ring measurements with unique repeated inventory data to study species mixing effects on growth responses during and after a drought (resistance, recovery and resilience) with a fine spatiotemporal resolution for past drought events occurring within the last 90 years. Individual tree neighbourhoods were characterized in terms of diversity and competition exerted by each species. Neighbourhood effects on drought responses were then analysed relative to tree age and size. Species constituting the target and neighbourhood trees were European beech (*Fagus sylvatica* L., hereafter beech), Norway spruce (*Picea abies* (L.) H. Karst, hereafter spruce) and silver fir (*Abies alba* Mill., hereafter fir).

Our main hypothesis was that species diversity positively influences an individual tree's drought response. However, the mixing effect is modulated by the identity of neighbouring species. Moreover, a tree's growth responses depend on its age and size, and the stand density.

## MATERIAL & METHODS

### Study Sites and Data Collection

A total of 255 trees were sampled from three long-term permanent plots in Switzerland: Crêt Rond, Dürsrüti and Le Chenit (Figure 1). These three plots are among the oldest and best documented permanent plots in the world and are part of the
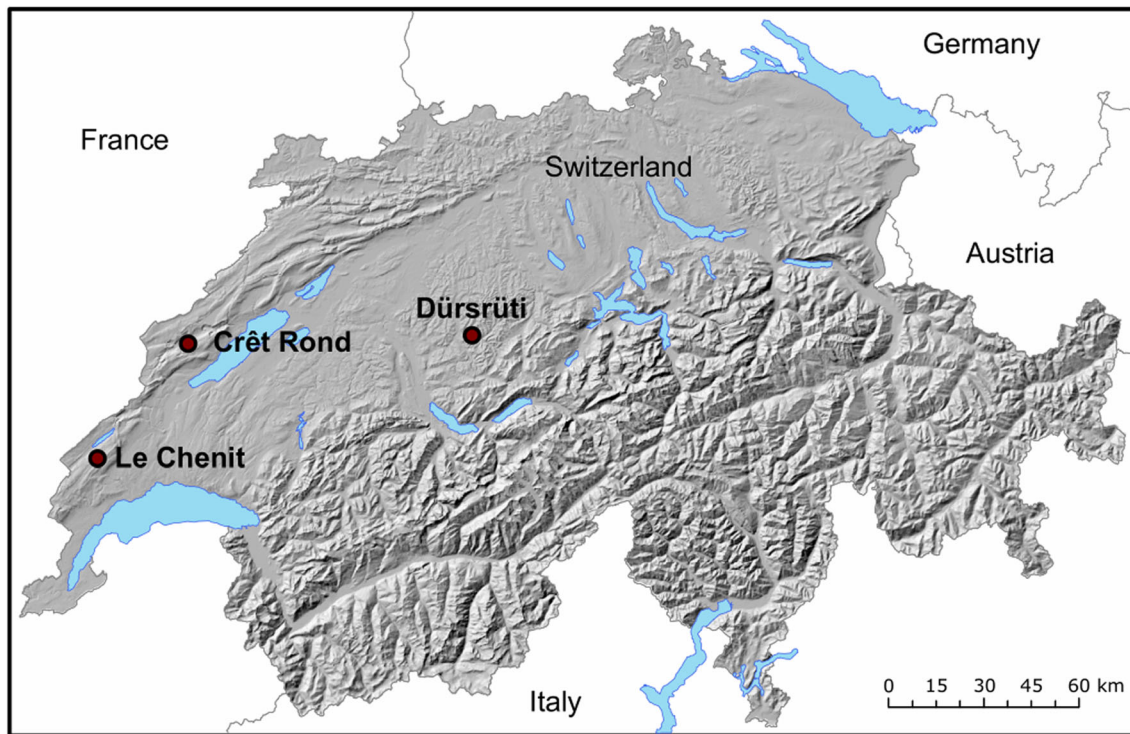
**Figure 1.** Location of the study sites in Switzerland.

Experimental Forest Management (EFM) project, which has been monitoring forest growth and yield since 1887 and currently counts 495 plots across Switzerland (Forrester and others 2019). For the present study, we selected plots monitored for approximately 100 years and which are composed of beech, fir and spruce (Table 1). All plots are managed following the plenter system (single tree selection), which means most trees experienced irregular growth through time because of succeeding suppression and competitive release phases until reaching (co-) dominance.

Around 30 trees were sampled per species and per plot for dendrochronological analyses (Table 2), except for Le Chenit where only 15 suitable beech trees were sampled. Within each plot, trees were selected based on their social status (dominant or codominant), to maximize the number of tree rings and to reduce ontogenetic effects on tree-ring series. Note that the sampled trees were not dominant or codominant over the whole inventory period and belonged to lower dominance classes earlier in their life according to their diameter development (Figure S1). To reduce our impact on the ongoing long-term monitoring at EFM plots, trees were sampled not only within the plot, but also from the buffer zone (same management regime and within five meters of the plot boundary).

For each tree, we extracted two cores at opposing directions and perpendicular to the slope with an increment borer. Cores were taken at about 0.5 m above ground to minimize financial loss due to reduced timber quality following coring. The DBH was strongly positively correlated with tree height over the whole inventory period (Spearman's $\rho = 0.83$, $p < 0.0001$) and can be considered as a reliable proxy for tree size without independently influencing the drought response.

## Tree-Ring Measurement and Chronology Development

Increment cores were processed according to standard dendrochronological procedure (Speer 2009). Tree cores were mounted and glued on wooden supports and air-dried. To distinguish tree-ring boundaries precisely, cores were subsequently sanded using sandpaper with progressively finer grit. Total ring width was measured with 0.01 mm precision using a Lintab digital positioning table coupled to the software TSAP (Rinntech, Heidelberg, Germany). For cores that missed the pith, tree age was estimated based on the width of the last incomplete ring, the length of its intersection with the core's border and the average width of the three previous rings according to the method of Duncan (1989). The two cores per tree were

**Table 1.** Main Plot Characteristics.

|  | Crêt Rond | Dürsrüti | Le Chenit |
|---|---|---|---|
| Biogeographical region | Jura | Prealps | Jura |
| Coordinates | 46°53′00″N, 6°33′34″E | 46°33′32″N, 6°13′19″E | 46°57′34″N, 7°46′25″E |
| Mean annual temperature (°C) | 7.2 | 7.1 | 5.1 |
| Mean annual precipitation sum (mm) | 1399 | 1436 | 1775 |
| Elevation (m a.s.l.) | 970 | 894 | 1340 |
| Plot area (ha) | 1.00 | 3.58 | 2.00 |
| Slope (%) | 20.9 | 15.2 | 10.6 |
| Aspect (°) | 337 | 338 | 186 |
| Soil characteristics | Rather shallow, low water-holding capacity, low nutrient concentration | Deep, good water-holding capacity and high nutrient concentration | Rather shallow, average water-holding capacity, average nutrient concentration |
| Monitored since | 1913 | 1914 | 1925 |
| Species composition (% of total basal area): |  |  |  |
| *F. sylvatica* | 28 | 21 | < 5 |
| *A. alba* | 54 | 39 | 7 |
| *P. abies* | 18 | 38 | 85 |

**Table 2.** Average Tree Characteristics at the Time of Sampling (2018).

|  |  | Number of cored trees | Age (range) | DBH in cm (range) | Height in m (range) | Crown area in m$^2$ (range) |
|---|---|---|---|---|---|---|
| Crêt Rond | Beech | 29 | 121 (78–235) | 36 (24–63) | 28 (23–35) | 49 (21–82) |
|  | Fir | 31 | 110 (72–197) | 53 (38–70) | 33 (24–38) | 32 (12–77) |
|  | Spruce | 26 | 233 (202–295) | 65 (55–73) | 38 (28–47) | 23 (11–74) |
| Dürsrüti | Beech | 30 | 123 (81–181) | 46 (34–64) | 29 (17–39) | 103 (53–152) |
|  | Fir | 31 | 129 (59–213) | 61 (35–99) | 33 (23–48) | 42 (20–74) |
|  | Spruce | 30 | 129 (52–237) | 56 (37–89) | 35 (25–48) | 42 (18–89) |
| Le Chenit | Beech | 17 | 130 (39–305) | 19 (8–54) | 14 (9–21) | 30 (14–45) |
|  | Fir | 29 | 157 (92–263) | 33 (18–45) | 18 (8–26) | 26 (8–57) |
|  | Spruce | 32 | 212 (116–345) | 48 (36–63) | 26 (21–32) | 19 (6–40) |

*DBH = diameter at breast height (1.3 m)*

used for mutual crossdating and pooled as to obtain an average tree-ring chronology. Next, tree-ring series were visually crossdated and statistically checked using the program COFECHA (Holmes 1983). To remove non-climatic growth trends while retaining a large year-to-year variability suited for our analyses (Fritts 2001), chronologies were detrended with a set of cubic smoothing splines of different time intervals (16, 32 and 64 years). Because of the irregular growth intrinsic to plenter systems, a spline of 16 years was most

suitable and applied to all chronologies using the package 'dplR' (Bunn 2008) in the statistical program R (R Core Team 2019).

## Climate Data and Drought Year Selection

Spatially interpolated daily climate data were obtained from the DAYMET model (Thornton and others 1997), spanning the period 1930–2017 and with a 100 m resolution. The DAYMET model utilizes a digital elevation model (100 m grid size) to

interpolate climate data from MeteoSwiss stations surrounding the study sites. Climate data included daily precipitation sum, mean temperature, minimum and maximum temperature and total solar radiation. We also calculated the standardized precipitation evapotranspiration index (SPEI) following Vicente-Serrano and others (2010). Monthly potential evapotranspiration (PET) was estimated based on monthly mean minimum and maximum temperatures, precipitation sum and latitude (proxy for solar radiation) using the Hargreaves equation (Hargreaves and Samani 1985). The monthly climatic water balance values used for the calculation of the SPEI (Vicente-Serrano and others 2010) were estimated by subtracting PET from precipitation. The SPEI provides a measure for aggregated water balance over multiple months or years. The more negative the value, the more severe the drought relative to average growing conditions at a certain site.

To identify the aggregation timescale of SPEI that correlates best with tree-ring chronologies, correlation analyses were replicated for each species and at each site for different aggregation timescales ranging from one to 24 months using the R package treeclim (Zang and Biondi 2015). Correlation coefficients were also used to identify the months or seasons when SPEI best reflects radial growth. On average, the timescale and month combination that had the highest influence on ring widths was five months (SPEI5) and the month of July (Supplementary Figure S2), respectively. Further, the SPEI5 of July (hereafter SPEI5$_{July}$), which includes the period from March to July in its calculation, covers the period of highest growth activity for trees in our study region and represents the period in which most of the water is taken up by trees (Brinkmann and others 2018b; Dietrich and others 2018; Vitasse and others 2019a). The SPEI5$_{July}$ values were thus used to identify the most severe droughts since 1930 (Figures 2 and 3). Years with SPEI5$_{July}$ below − 1 were considered drought years and had values ranging from − 1.03 (2017; relatively mild drought) to − 2.01 (1976; relatively severe drought). Selected drought years were pooled in subsequent analyses and their severities were considered by including their SPEI5$_{July}$ values in the models.

## Competition and Diversity Indices

The inventory data for the three sites reach at least beyond 1925, and the plots have been measured every seven to nine years on average since then. Although dendrometric measurements have been performed since the establishment of the plots, individual trees have been reliably georeferenced only since 1970. Therefore, we restricted the neighbourhood competition analyses from that date onward. Neighbourhood analyses were done in R with the package 'sf' (Pebesma 2018). All neighbouring trees within less than 10 m of the target tree were used to calculate a distance-dependent competition index using the following equation (Forrester and others 2013):

$$NI_i = \sum_{j=1}^{n} \frac{\text{basal, , area}_j}{\text{distance}_{ij}}$$

where NI$_j$ is the neighbourhood competition experienced by the target tree ($i$) based on the basal area (cm$^2$) and distance (m) of its $n$ neighbours. This simple competition index was calculated for the competition exerted by each of the neighbouring species individually, generating the following indices: NI$_b$ (beech), NI$_f$ (fir) and NI$_s$ (Spruce). A radius of 10 m was selected because it maximizes the $R^2$ of the relationship between the basal area increment and the competition index (Forrester and others 2013).

Based on the same neighbour trees selected for the computation of the above competition index, a measure of diversity was obtained based on Shannon's index (Shannon and Weaver 1948):

$$H' = -\sum_{i=1}^{S} p_i \ln(p_i)$$

where p$_i$ is the proportion of species $i$ in the target tree's neighbourhood composed of $S$ species.

## Components of Drought Resilience

Growth responses to drought were quantified using the components of drought resilience described by Lloret and others (2011), which break down growth resilience into three components reflecting growth before, during and after a drought event:

$$\text{Resistance} = \frac{\text{Dr}}{\text{preDr}}; \text{Recovery} = \frac{\text{postDr}}{\text{Dr}};$$
$$\text{Resilience} = \frac{\text{postDr}}{\text{preDr}}$$

where preDr, Dr and postDr equal ring width index before, during and after a drought year, respectively. We used the average ring width index of 2 years before and after a drought for preDr and postDr, respectively, to include lagged growth responses (Gazol and others 2017). We restricted this period to two years before and after the selected
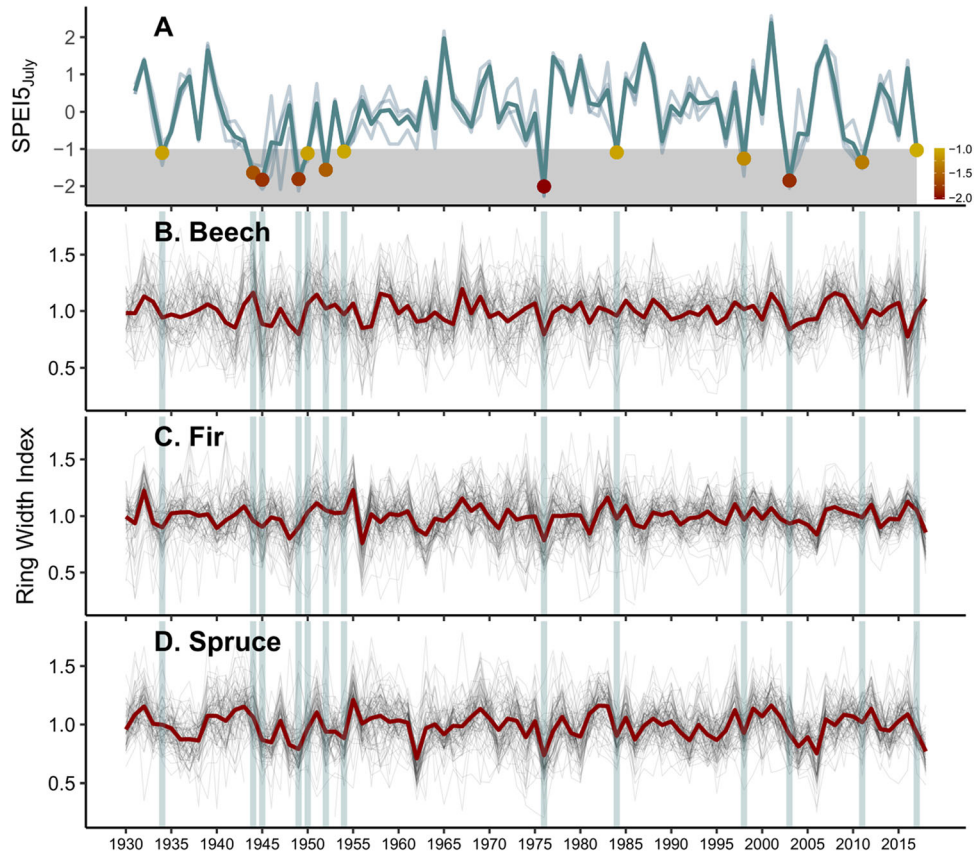
**Figure 2.** Time series of SPEI$_{July}$ aggregated over 5 months (**A**) and tree rings width index chronology for beech (**B**), fir (**C**) and spruce (**D**). Light grey chronologies represent site-specific SPEI$_{July}$ time series (**A**) and all individual tree rings width index chronologies (**B–D**), respectively. Coloured dots in panel **A** indicate drought years according to drought severity based on SPEI$_{July}$ values. Vertical grey lines (**B–D**) represent selected drought years. See Figure S3 for site-specific chronologies.

droughts to avoid the influence of consecutive droughts and potential growth depressions due to mast events that occurred, for example, in 2006 (Ascoli and others 2017; Schwarz and Bauhus 2019).

## Statistical Analyses

Initially, nonparametric Kruskal–Wallis tests were used to detect differences in drought response (resistance, recovery, resilience) among species and sites, thus prior to accounting for other variables of interest. This was followed by a Wilcoxon rank-sum test with a Bonferroni correction for multiple testing to assess pairwise differences between groups (Table S1).

In a second step, linear mixed effects models were used to assess the influence of competition on the different drought response components per species. Because neighbourhood competition indices could only be computed for inventory years from 1970 onward (once trees were accurately georeferenced),

the mixed models only cover droughts occurring in this period (that is, 1976, 1984, 1998, 2003, 2011 and 2017). The predictors include the spatially explicit neighbourhood competition indices NI$_b$, NI$_f$ and NI$_s$, Shannon diversity values, tree age, DBH and SPEI5$_{July}$. We also initially included an interaction term between the Shannon diversity index and SPEI5$_{July}$ as predictor, but the interaction term was only significant in one out of nine cases (Table S2). The interaction term was thus left out from the model to reduce its complexity. We ran the model for each species separately, to separate intra- from interspecific competition and to compare neighbourhood effects between all species pairs (Table 3). To compare overall drought responses between species, an overarching model with a categorical species variable was constructed (Table S3). This reinforces the Kruskal–Wallis test (Table S1) as the linear mixed effect model accounted for variation caused by tree age, DBH, SPEI5$_{July}$ neighbourhood competition and diversity.
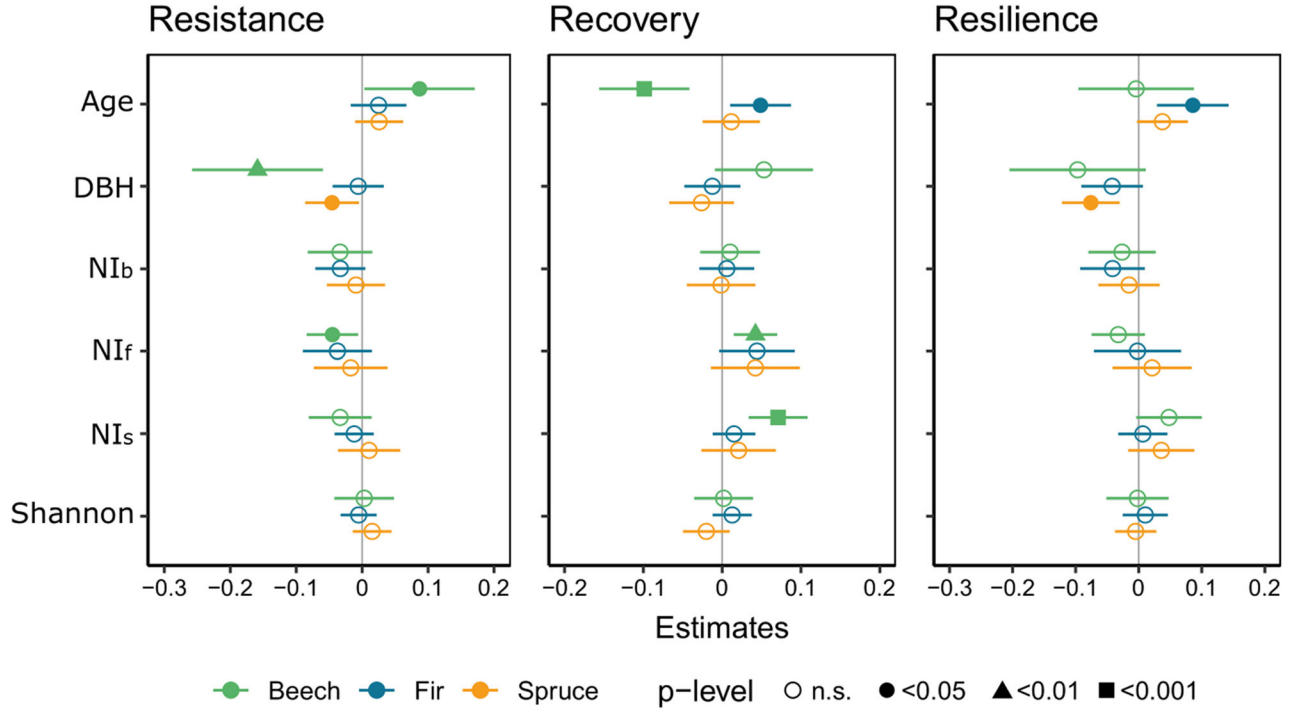
**Figure 3.** Forest plot illustrating effect sizes of variables according to the model with droughts since 1970. See Table 3 for more details.

For variables expected to gradually change between inventories (that is, age and DBH), values were linearly interpolated within inventory intervals using the R package '*imputeTS*' (Moritz and Bartz-Beielstein 2017). Predictor variables were centred and scaled to allow direct mutual comparison of effect sizes.

Response variables were log-transformed for normality in all models. We verified the presence of multicollinearity among the predictors using the variance inflation factor (VIF) with the *vif* function of the R package '*car*' (Fox and Weisberg 2019). Variables with VIF greater than 3 were discarded. To identify the best random structure, we compared a generalized least-squares model to linear mixed models with different random terms using the restricted maximum likelihood method (Zuur and others 2009). In all cases, the best random structure was drought year nested in plots. This compensates for the unmeasured variation related to differences between sites and drought years. Resulting models constructed are shown in Eq. (1).

$$y = \beta_0 + \beta_1 \text{Age}_i + \beta_2 \text{DBH}_i + \beta_3 \text{SPEI5}_{\text{July},i} + \beta_4 N_{b,i} \\ + \beta_5 N_{f,i} + \beta_6 N_{s,i} + r_i + \varepsilon_i$$

(1)

where $y$ represents the response variable $i$ (Rt, Rc or Rs). $\beta_0$ is the intercept, $\beta_{1-6}$ are parameter coeffi-

cients, $r_i$ is the random effect (drought year nested in site) and $\epsilon_i$ is the residual variation.

A pseudo-R-squared for mixed effect models was used to determine the variance explained by both the fixed terms only (marginal coefficient of determination, $R_m^2$) and the entire model including the random terms (conditional coefficient of determination, $R_c^2$) using the R package '*Mumln*' (Nakagawa and Schielzeth 2013; Barton 2019). Model residuals were visually inspected for normality and homoscedasticity. Mixed effect models were ran using the package '*nlme*' (Pinheiro and others 2018). All analyses were done in R (R Core Team 2019).

## RESULTS

### Species-Specific Drought Responses

Generally, radial growth responded substantially and consistently to the different droughts over time, albeit dependent on the drought severity (Figure 2). The 1940s were characterized by a sequence of successive severe and mild droughts and blurred growth responses, especially for mild droughts occurring after severe droughts.

The significant positive effect of SPEI5$_{\text{July}}$ on resistance of spruce in the models (Table 3, Figure 3) confirmed the importance of drought severity on growth resistance. Although SPEI5$_{\text{July}}$

**Table 3.** Linear Mixed Model Output Including Droughts Since 1970 (that is, 1976, 1984, 1998, 2003, 2011 and 2017).

| | | Response (log-transformed) | | |
| --- | --- | --- | --- | --- |
| | | Resistance | Recovery | Resilience |
| Beech | Intercept | 0.105 (0.204) | 0.114 (0.067) | 0.192 (0.213) |
| | Age | 0.087* (0.042) | − 0.099*** (0.029) | − 0.004 (0.047) |
| | DBH | − 0.159** (0.050) | 0.053 (0.032) | − 0.097 (0.055) |
| | $NI_b$ | − 0.034 (0.025) | 0.010 (0.019) | − 0.027 (0.027) |
| | $NI_f$ | − 0.045* (0.020) | 0.042** (0.014) | − 0.032 (0.022) |
| | $NI_s$ | − 0.033 (0.024) | 0.071*** (0.019) | 0.048 (0.026) |
| | Shannon | 0.003 (0.023) | 0.002 (0.019) | − 0.002 (0.025) |
| | $SPEI5_{July}$ | 0.228 (0.115) | − 0.028 (0.041) | 0.187 (0.112) |
| | Observations | 267 | 267 | 268 |
| | $R^2_m$ | 0.11 | 0.11 | 0.10 |
| | $R^2_c$ | 0.50 | 0.13 | 0.51 |
| Fir | Intercept | 0.192 (0.136) | − 0.081 (0.128) | 0.101 (0.124) |
| | Age | 0.025 (0.021) | 0.049* (0.020) | 0.086** (0.029) |
| | DBH | − 0.006 (0.020) | − 0.012 (0.018) | − 0.042 (0.025) |
| | $NI_b$ | − 0.033 (0.019) | 0.006 (0.018) | − 0.042 (0.026) |
| | $NI_f$ | − 0.038 (0.027) | 0.044 (0.024) | − 0.002 (0.035) |
| | $NI_s$ | − 0.012 (0.015) | 0.015 (0.014) | 0.007 (0.020) |
| | Shannon | − 0.005 (0.014) | 0.013 (0.013) | 0.010 (0.018) |
| | $SPEI5_{July}$ | 0.180 (0.084) | − 0.120 (0.079) | 0.055 (0.058) |
| | Observations | 299 | 298 | 298 |
| | $R^2_m$ | 0.11 | 0.07 | 0.07 |
| | $R^2_c$ | 0.40 | 0.39 | 0.33 |
| Spruce | Intercept | 0.128 (0.140) | 0.034 (0.181) | 0.184 (0.208) |
| | Age | 0.026 (0.018) | 0.012 (0.018) | 0.038 (0.020) |
| | DBH | − 0.046* (0.021) | − 0.026 (0.021) | − 0.076** (0.023) |
| | $NI_b$ | − 0.009 (0.022) | − 0.001 (0.022) | − 0.015 (0.025) |
| | $NI_f$ | − 0.017 (0.028) | 0.042 (0.029) | 0.021 (0.032) |
| | $NI_s$ | 0.010 (0.024) | 0.021 (0.024) | 0.036 (0.027) |
| | Shannon | 0.015 (0.015) | − 0.020 (0.015) | − 0.005 (0.017) |
| | $SPEI5_{July}$ | 0.186* (0.076) | − 0.071 (0.112) | 0.126 (0.127) |
| | Observations | 292 | 292 | 292 |
| | $R^2_m$ | 0.10 | 0.03 | 0.07 |
| | $R^2_c$ | 0.42 | 0.43 | 0.48 |

*Three models per species were constructed according to the three components of resilience (Lloret and others 2011) as log-transformed variables. $SPEI5_{July}$ = standardized precipitation evapotranspiration index (SPEI) of the month of July with an aggregation period of 5 months. DBH = diameter at breast height. Neighbourhood competition indices are represented by $NI_b$, $NI_f$ and $NI_s$ for beech, fir and spruce, respectively. Shannon = Shannon diversity index. Significance levels:\*p < 0.05; \*\*p < 0.01; \*\*\*p < 0.001.*

effects were non-significant for recovery and resilience components, effect sizes were generally large and always positive for resilience.

The drought response varied significantly among species. The models for species comparisons (Table S3) indicated a higher drought resistance and resilience of fir than beech and spruce. Spruce appeared to be slightly more drought resistant than beech. Nonparametric tests confirmed these trends, with significant differences among species for resistance (Kruskal–Wallis $\chi^2$ = 38.72, p < 0.0001)

and resilience ($\chi^2$ = 35.85, p < 0.0001), but not for recovery ($\chi^2$ = 1.25, p = 0.536). Note that responses also significantly differed between sites for recovery ($\chi^2$ = 8.17, p = 0.017) and resilience ($\chi^2$ = 12.89, p = 0.002), but especially resistance ($\chi^2$ = 58.03, p < 0.0001) (Figure 4). See Table S1 in appendix for pairwise comparisons.

## Effects of Tree Age and Size

Significant effects were found for both age and size, but with important interspecific differences (Ta-
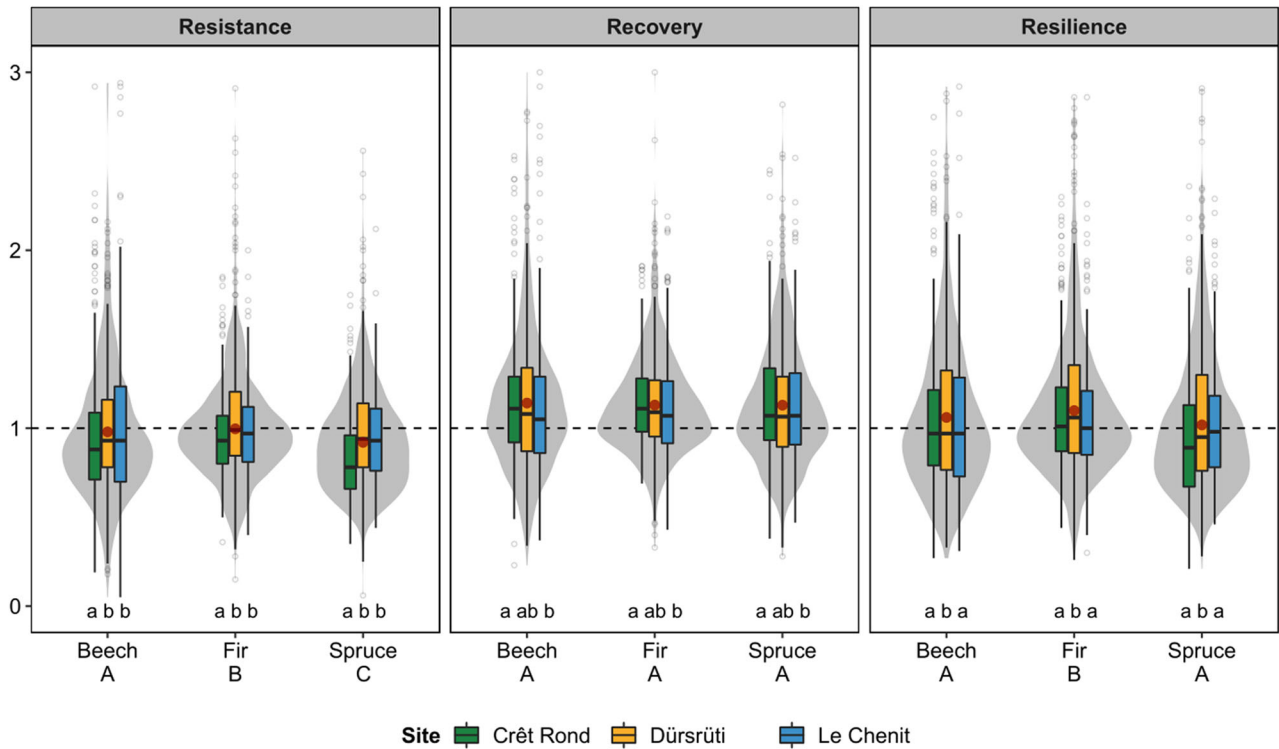
**Figure 4.** Boxplot of differences in drought components as defined by Lloret and others (2011) according to species and sites. The grey shape represents the overall distribution of responses, joining the three sites together, and the red dot represents the mean response.

ble 3, Figure 3). For beech, age had a significant positive effect on resistance, but a negative effect on recovery and size had a significantly negative effect on resistance. The recovery and resilience of fir were significantly positively influenced by age, but size had no significant effect. For spruce, in contrast, age effects were never significant, but size had a significant negative effect resistance and resilience. Size had a predominantly negative effect on drought responses, except for the recovery of beech.

## Effects of stand density and neighbourhood characteristics

The neighbourhood indices ($NI_b$, $NI_f$ and $NI_s$, Table 3, Figure 3) yielded few significant effects for all of the drought resilience components, with significant effects only detected for the drought response of beech. Here, $NI_f$ had a significant negative effect on resistance, while both $NI_f$ and $NI_s$ had a significant positive effect on recovery. In eight out of nine cases, competition indices have negative coefficients when it comes to resistance, but positive coefficients for recovery. The Shannon diversity index had exclusively small effect sizes, none of which were significant.

## DISCUSSION

We used a unique combination of tree-ring and repeated forest inventory data collected in three of the oldest permanent forest monitoring plots in Central Europe to assess the effect of neighbourhood competition and species diversity on the drought resilience of beech, spruce and fir. Tree growth responses to a selection of six droughts that occurred over the period 1970–2018 were quantified as a function of neighbourhood characteristics, tree age and tree size.

## Effect of Neighbourhood Competition and Diversity

Overall, neighbourhood characteristics had weak and species-specific effects on drought resilience indices. Only the drought resistance and recovery of beech were significantly influenced by interspecific competition. Species diversity, as quantified by the Shannon index, never had a significant effect in any of the models. Taken together, these elements refute our main hypothesis that a diverse neighbourhood would be beneficial to mitigate growth responses during drought responses. This finding agrees with the study of Schwarz and

Bauhus (2019) who reported no clear advantages of mixing fir and beech to mitigate growth responses to droughts, except that beech might improve its recovery when mixed with fir. We also found a similar response for beech recovery when beech was mixed with fir and/or spruce. Overall, this weak diversity effect on growth responses to drought seems counter-intuitive because one might expect interspecific competition for resources to be relatively more advantageous than intraspecific competition under which conspecifics display nearly identical traits (Hooper and others 2005; Gazol and Camarero 2016).

Beech may be benefitting from growing in neighbourhoods consisting of spruce because spruce is more shallow-rooting than the two other species (Leuschner and Ellenberg 2017), leaving more opportunities for interspecific competitors to acquire deeper soil water (Pretzsch and others 2013a). Beech trees can also increase their water uptake depth as a function of water availability, in contrast to spruce (Brinkmann and others 2018a). Additionally, differences in rooting traits may allow a more complete occupation of the soil space (Brassard and others 2011), leading to a potentially more extensive use of soil water.

During droughts, beech, being the most anisohydric of the three species (Stokes and Norris 2007; Pretzsch and others 2013b; Leuschner and Ellenberg 2017), may also benefit from a neighbourhood composed of fir and spruce because of temporal differences in water uptake. Isohydric species such as fir and especially spruce, close their stomata earlier during droughts to reduce the risk of cavitation (Jones and Sutherland 1991; Hartmann 2011), which may leave more opportunities for neighbouring anisohydric trees (that is, beech) to acquire water until later phases of the drought (Pretzsch and others 2013a). In this case, an increased resistance for beech might be expected, contradicting the negative influence of fir competition found in our study. The positive effect of a fir and spruce neighbourhood appears mostly on beech recovery. One possible reason is that the recovery of isohydric species is impaired during particularly long-lasting droughts, which can lead to carbon starvation because reserves are being depleted without being restored (Hartmann 2011). A potential delay in fir and spruce recovery might therefore favour beech recovery. Another mechanism related to temporal variation in water use is phenological differences in growth onset, such as between evergreen and deciduous species, which may lead to an earlier water uptake and an

advantage in terms of drought resilience in the long term (Jourdan and others 2019).

The literature concerning mixing effects on drought response of these three species varies in its outcomes. Similar to our results, beech was found to perform better in terms of resistance and resilience when growing with spruce based on both basal area increment (Pretzsch and others 2013a) and $^{13}C$ discrimination (Schäfer and others 2017). Conversely, a recent study found fir to be the only species experiencing a positive effect on all three resilience components from growing with beech and spruce (Bosela and others 2019). Similarly, fir resistance and resilience were positively influenced when growing with spruce, whereas spruce itself was negatively impacted in a study in south-western Germany (Vitali and others 2018). In the same line, but looking from the perspective of neighbourhood functional diversity (up to six species), fir recovery and resilience benefited from increased diversity in the Pyrenees (Gazol and Camarero 2016).

Diversity effects on drought resilience of these three species, but also more generally, are surprisingly inconsistent. In theory, a positive effect is expected because of both facilitation and competitive reduction, which may result from hydraulic redistribution (that is, facilitation), temporal partitioning of soil water availability between isohydric and anisohydric species or species with contrasting phenologies and the spatial partitioning of soil water through different rooting depths and structures (that is, competitive reduction) (Pretzsch and others 2014; Forrester and others 2016; Ammer 2018). Yet, a recent review found that only 42% of studies reported exclusively positive mixing effects on drought sensitivity (Grossiord 2018), with the remaining studies most frequently finding mixed effects (Lebourgeois and others 2013; Grossiord and others 2014; Forrester and others 2016; Metz and others 2016; Vitali and others 2018; Jourdan and others 2019; Vanhellemont and others 2019). Again, many of those inconsistencies are likely related to the interaction between species identity effects and local site conditions (Pretzsch and others 2017; Ammer 2018), and the rather important differences in drought responses are found between sites further substantiate this rationale (Table S1).

## Effects of Tree Age and Size

The presence of age effects for beech and fir, but not for spruce, suggests a species specificity when it comes to age effects. While spruce appears unaffected, fir's drought responses ameliorate with

increasing age and beech experiences mixed effects. These contradictory results are echoed in the literature, as research has similarly found no age effects (Esper and others 2008), but also both increasing (Primicia and others 2015) and decreasing (Rozas and others 2009) climate sensitivity with increasing age. These studies are, however, all based on different species and relate to long-term changes in sensitivity, not to growth responses during extreme droughts. Zang and others (2014) examined age effects on drought responses using the same drought resilience components and for the three same species with comparable meanages, but found a clear increase in vulnerability with age in all species. Increased drought sensitivity with increasing age might be ascribed to decreasing photosynthetic activity or cellular senescence (Yoder and others 1994; Mencuccini and others 2005; Ding and others 2017b), even though this is likely negligible when compared to the effect of tree size and there is little evidence to support the cellular senescence hypothesis (Mencuccini and others 2005). It is important to note that we only sampled codominant and dominant trees that were present in the plots in 2018 and that old trees that may have exhibited decreasing growth vitality or even mortality in the past following drought events may have been harvested or outcompeted, hence possibly introducing a survivor bias (Brienen and others 2012; Teets and others 2018). Unfortunately, the effect and causes of tree mortality (if any) could not be included in our analysis because unvital trees in plenter forests are normally removed prior to death. However, we believe that such bias is minimal and was compensated by the large range in tree age and size included in our analysis.

In contrast to the mixed age effects, tree size consistently negatively influenced drought responses, albeit not always significantly. Only beech size appeared to influence recovery positively but non-significantly. Contrasting results are also reported in the literature when it comes to the effect of tree size and social status, with increased sensitivity reported for both large and small trees, or no effect at all (see Bello and others 2019; Mérian and Lebourgeois 2011 and references therein). Yet, a trend of increasing drought sensitivity with increasing size does appear more common at a global scale, as found in a meta-analysis (Bennett and others 2015). Considering the species studied in our study specifically, larger beech and fir trees were found to be more sensitive, but not spruce (Mérian and Lebourgeois 2011). In contrast, and based on dendroecological analyses similar to ours,

Ding and other (2017) found a negative size effect on sensitivity in spruce, but not in beech, supporting the results of a simulation study (Rötzer and others 2017).

According to our results, size is most disadvantageous to spruce, followed by beech and then fir. Despite the fact that only (co-)dominant individuals were sampled in our study at the time of sampling, a large range in sizes and social statuses is nonetheless present in our analyses as indicated by the forest inventory data that covered the last 90 years. It may be nonetheless prudent to mention that an interplay between tree age, size and site conditions might exist, a potentially confounding factor that we decided not to investigate for the sake of simplicity.

Mechanisms behind tree size effects on drought sensitivity are manifold and have contrasting outcomes. Even in the absence of species differences, intraspecific differences in tree size can strongly influence the interactions between trees as indicated by the shapes (for example, concave, linear or exponential) of relationships between tree size and resource uptake, resource-use efficiency or drought stress (Forrester 2019). This not only modifies the overall stand-level responses (Forrester 2019), but also limits the value of trait-based interpretations of identity or species diversity effects. On the one hand, large trees can be more affected by drought because of (1) their increased exposition to direct sunlight leading to higher transpiration in the summer, (2) a higher architectural complexity leading to increased hydraulic resistance over the longer path length and lowered photosynthetic rates, (3) wider water-transporting conduits increasing the chance of embolisms and (4) a higher probability to be attacked by bark beetles following droughts (Mencuccini and others 2005; Mérian and Lebourgeois 2011; Bennett and others 2015; Olson and others 2018). On the other hand, this disadvantage could be partially mitigated because of their greater potential to reach deeper soil water reserves using a more expansive root network (Mérian and Lebourgeois 2011; Bello and others 2019).

Regardless of the ambiguous results found in the literature for both tree age and size effects, a more consistent finding is that size effects often overshadow age effects (Mencuccini and others 2005; Schwarz and Bauhus 2019), which is not supported by our findings. When investigating climate sensitivity and growth responses to extreme droughts, we therefore recommend including both a measure of age as well as to consider tree dimensions, whenever possible.

## Species-Specific Drought Responses

According to both sets of models, our results indicate that fir is significantly more resistant and resilient to drought compared to beech and spruce, but does not perform better in terms of recovery. This matches findings by Zang and others (2014) and supports the assumption that fir is more drought-tolerant overall (Tinner and others 2013; Leuschner and Ellenberg 2017; Vitali and others 2017; Vitasse and others 2019b). Indeed, paleoecological and dendroecological research points towards its potential to cope with a future warmer and drier climate in Central Europe when growing on soil with sufficient water retention capacity, which may partially be attributed to its taproot being able to access deep soil layers (Vitasse and others 2019b). There are nonetheless exceptions, such as towards the driest and southernmost distribution limit of silver fir where its growth declined following the recent increase in aridity (Gazol and others 2015; Sánchez-Salguero and others 2017).

When comparing drought responses of beech with spruce, their tolerance appears generally similar although a marginally better performance of spruce was found (Table S3). Both beech and spruce are particularly sensitive to drought (Kolář and others 2017; Leuschner and Ellenberg 2017) although, in contrast to our findings, spruce is generally considered more vulnerable, especially when planted far outside its natural range (Ding and others 2017b; Leuschner and Ellenberg 2017; Schäfer and others 2017; Bosela and others 2019). More specifically, spruce is thought to have a lower resistance, but a higher recovery than beech, which could be attributed to its isohydric character (Pretzsch and others 2013a).

## Implications for Management and Further Research

We found weak evidence of the importance of species diversity for drought resilience. Although our approach combines a large timescale with precise tree neighbourhood information and effectively incorporates identity effects, the narrow range in site conditions may limit the generalization of our conclusions. Nevertheless, since each selected species has different ecological needs, the variation in suitable sites where these ecological needs intersects quickly narrows down with an increasing number of species. Ideally, studies would have to include sites covering a large range of site conditions, where the same set of species would occur with a high within-site variability in species proportions and density. A major challenge for future research is thus to find the same species assemblage occurring under both mesic and xeric conditions as to include both species identity and site condition effects, while accounting for differences in stand density.

Considering the paucity of robust evidence of a strong species diversity effect on drought resilience (Bauhus and others 2017), increasing diversity regardless of the species identity and site conditions does not provide a silver bullet for guaranteeing the enhanced resilience of forests to climate change. Other strategies such as density reduction and management through thinning appear to have reached more scientific consensus (Giuggiola and others 2013; Sohn and others 2016; Bottero and others 2017) and would be more advisable based on current knowledge. Still, this line of research improves our understanding of mixing effects on drought resilience and contributes to pinpointing mixtures (species and species proportions) of particular interest, especially through reviews such as done by Grossiord (2018). In fact, the identification of specific mixtures most resilient to climate change was found to be the number one concern raised by European forest managers (Coll and others 2018). Even though current research remains ambiguous about positive interspecific synergies playing a role during extreme droughts, species mixing nevertheless has the advantage of spreading the risk over multiple species (insurance hypothesis, see Bauhus and others 2017; Yachi and Loreau 1999) and stabilizing forest growth during drought events through asynchronous responses (Vanhellemont and others 2019). At last, increasing species and functional diversity can assure the fulfilment of a multitude of forest functions and ecosystem services such as carbon storage, biodiversity, recreation and timber production (Gamfeldt and others 2013; Brockerhoff and others 2017; Schuler and others 2017; Coll and others 2018), and should therefore be aimed for regardless of the potential increase in drought tolerance.

their constructive comments which significantly improved our manuscript.

## DATA AVAILABILITY

The EFM data are available upon request from David Forrester and the tree-ring data from Mathieu Lévesque.

## REFERENCES

Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears DD, Hogg EH (Ted., Gonzalez P, Fensham R, Zhang Z, Castro J, Demidova N, Lim JH, Allard G, Running SW, Semerci A, Cobb N. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For Ecol Manage 259:660–84.

Ammer C. 2018. Diversity and forest productivity in a changing climate. New Phytol. https://doi.org/10.1111/nph.15263

Ascoli D, Maringer J, Hacket-Pain A, Conedera M, Drobyshev I, Motta R, Cirolli M, Kantorowicz W, Zang C, Schueler S, Croisé L, Piussi P, Berretti R, Palaghianu C, Westergren M, Lageard JGA, Burkart A, Gehrig Bichsel R, Thomas PA, Beudert B, Övergaard R, Vacchiano G. 2017. Two centuries of masting data for European beech and Norway spruce across the European continent. Ecology.

Aussenac R, Bergeron Y, Gravel D, Drobyshev I. 2018. Interactions among trees: a key element in the stabilising effect of species diversity on forest growth. Funct Ecol. https://doi.org/10.1111/1365-2435.13257

Barton K. 2019. Package 'MuMIn'. R Package Version 1(43):6.

Bauhus J, Forrester DI, Gardiner B, Jactel H, Vallejo R, Pretzsch H. 2017. Ecological stability of mixed-species forests. In: Pretzsch H, Forrester D, Bauhus J, Eds. Mixed-Species Forests: Ecology and Management. Berlin : Springer.

Bello J, Vallet P, Perot T, Balandier P, Seigner V, Perret S, Couteau C, Korboulewsky N. 2019. How do mixing tree species and stand density affect seasonal radial growth during drought events? For Ecol Manage 432:436–45.

Bennett AC, Mcdowell NG, Allen CD, Anderson-Teixeira KJ. 2015. Larger trees suffer most during drought in forests worldwide. Nat Plants 1:1–5.

Biondi F. 1999. Comparing tree-ring chronologies and repeated timber inventories as forest monitoring tools. Ecol Appl 9:216–27.

Bosela M, Kulla L, Roessiger J, Šebeň V, Dobor L, Büntgen U, Lukac M. 2019. Long-term effects of environmental change and species diversity on tree radial growth in a mixed European forest. For Ecol Manage 446:293–303. https://linkinghub.elsevier.com/retrieve/pii/S0378112719304839

Bottero A, D'Amato AW, Palik BJ, Bradford JB, Fraver S, Battaglia MA, Asherin LA. 2017. Density-dependent vulnerability of forest ecosystems to drought. J Appl Ecol 54:1605–14.

Brassard BW, Chen HYH, Bergeron Y, Paré D. 2011. Differences in fine root productivity between mixed- and single-species stands. Funct Ecol 25:238–46.

Brienen RJW, Gloor E, Zuidema PA. 2012. Detecting evidence for CO 2 fertilization from tree ring studies: The potential role of sampling biases. Global Biogeochem Cycles.

Brinkmann N, Eugster W, Buchmann N, Kahmen A. 2018a. Species-specific differences in water uptake depth of mature temperate trees vary with water availability in the soil. Plant Biol 21:71–81.

Brinkmann N, Seeger S, Weiler M, Buchmann N, Eugster W, Kahmen A. 2018b. Employing stable isotopes to determine the residence times of soil water and the temporal origin of water taken up by *Fagus sylvatica* and *Picea abies* in a temperate forest. New Phytol 219:1300–13.

Brockerhoff EG, Barbaro L, Castagneyrol B, Forrester DI, Gardiner B, González-Olabarria JR, Lyver POB, Meurisse N, Oxbrough A, Taki H, Thompson ID, van der Plas F, Jactel H. 2017. Forest biodiversity, ecosystem functioning and the provision of ecosystem services. Biodivers Conserv 26:3005–35.

Bunn AG. 2008. A dendrochronology program library in R (dplR). Dendrochronologia 26:115–24.

Camarero JJ, Gazol A, Sangüesa-Barreda G, Oliva J, Vicente-Serrano SM. 2015. To die or not to die: Early warnings of tree dieback in response to a severe drought. J Ecol 103:44–57.

CH2018. 2018. CH2018—Climate Scenarios for Switzerland. Zurich: Technical Report.

Chamagne J, Tanadini M, Frank D, Matula R, Paine CET, Philipson CD, Svátek M, Turnbull LA, Volařík D, Hector A. 2017. Forest diversity promotes individual tree growth in central European forest stands. J Appl Ecol 54:71–9.

Coll L, Ameztegui A, Collet C, Löf M, Mason B, Pach M, Verheyen K, Abrudan I, Barbati A, Barreiro S, Bielak K, Bravo-Oviedo A, Ferrari B, Govedar Z, Kulhavy J, Lazdina D, Metslaid M, Mohren F, Pereira M, Peric S, Rasztovits E, Short I, Spathelf P, Sterba H, Stojanovic D, Valsta L, Zlatanov T, Ponette Q. 2018. Knowledge gaps about mixed forests: What do European forest managers want to know and what answers can science provide? For Ecol Manage 407:106–15. https://doi.org/10.1016/j.foreco.2017.10.055

Condés S, Sterba H, Aguirre A, Bielak K, Bravo-Oviedo A, Coll L, Pach M, Pretzsch H, Vallet P, del Río M. 2018. Estimation and uncertainty of the mixing effects on Scots Pine-European beech productivity from national forest inventories data. Forests 9.

del Río M, Pretzsch H, Ruíz-Peinado R, Ampoorter E, Annighöfer P, Barbeito I, Bielak K, Brazaitis G, Coll L, Drössler L, Fabrika M, Forrester DI, Heym M, Hurt V, Kurylyak V, Löf M, Lombardi F, Madrickiene E, Matović B, Mohren F, Motta R, den Ouden J, Pach M, Ponette Q, Schütze G, Skrzyszewski J, Sramek V, Sterba H, Stojanović D, Svoboda M, Zlatanov TM, Bravo-Oviedo A. 2017. Species interactions increase the temporal stability of community productivity in *Pinus sylvestris–Fagus sylvatica* mixtures across Europe. J Ecol 105:1032–43.

del Río M, Schütze G, Pretzsch H. 2014. Temporal variation of competition and facilitation in mixed species forests in Central Europe. Plant Biol 16:166–76.

Dietrich L, Zweifel R, Kahmen A. 2018. Daily stem diameter variations can predict the canopy water status of mature temperate trees. Tree Physiol 38:941–52.

Ding H, Pretzsch H, Schütze G, Rötzer T. 2017. Size-dependence of tree growth response to drought for Norway spruce and European beech individuals in monospecific and mixed-species stands. Plant Biol 19:709–19.

Duncan RP. 1989. An evaluation of errors in tree age estimates based on increment cores in Kahiketea (*Dacrycarpus dacrydioides*). New Zeal Nat Sci 16:31–7.

Esper J, Niederer R, Bebi P, Frank D. 2008. Climate signal age effects-Evidence from young and old trees in the Swiss Engadin. For Ecol Manage 255:3783–9.

Evans MEK, Falk DA, Arizpe A, Swetnam TL, Babst F, Holsinger KE. 2017. Fusing tree-ring and forest inventory data to infer influences on tree growth. Ecosphere 8.

Fichtner A, Härdtle W, Li Y, Bruelheide H, Kunz M, von Oheimb G. 2017. From competition to facilitation: how tree species respond to neighbourhood diversity. Ecol Lett 20:892–900.

Forrester D, Nitzsche J, Schmid H. 2019. The Experimental Forest Management project: An overview and methodology of the long-term growth and yield plot network. Birmensdorf: Swiss Federal Institute of Forest, Snow and Landscape Research WSL.

Forrester DI. 2014. The spatial and temporal dynamics of species interactions in mixed-species forests: From pattern to process. For Ecol Manage 312:282–92. https://doi.org/10.1016/j.foreco.2013.10.003.

Forrester DI. 2019. Linking forest growth with stand structure: Tree size inequality, tree growth or resource partitioning and the asymmetry of competition. For Ecol Manage 447:139–57. https://doi.org/10.1016/j.foreco.2019.05.053.

Forrester DI, Bauhus J. 2016. A Review of Processes Behind Diversity—Productivity Relationships in Forests. Curr For Reports 2:45–61.

Forrester DI, Bonal D, Dawud S, Gessler A, Granier A, Pollastrini M, Grossiord C. 2016. Drought responses by individual tree species are not often correlated with tree species diversity in European forests. J Appl Ecol 53:1725–34.

Forrester DI, Kohnle U, Albrecht AT, Bauhus J. 2013. Complementarity in mixed-species stands of Abies alba and Picea abies varies with climate, site quality and stand density. For Ecol Manage 304:233–42. https://doi.org/10.1016/j.foreco.2013.04.038.

Fox J, Weisberg S. 2019. An R Companion to Applied Regression. Thousand Oaks CA Sage: Third Edition.

Fritts HC. 2001. Tree Rings and Climate. Caldwell: Blackburn Press.

Gamfeldt L, Snäll T, Bagchi R, Jonsson M, Gustafsson L, Kjellander P, Ruiz-Jaen MC, Fröberg M, Stendahl J, Philipson CD, Mikusiński G, Andersson E, Westerlund B, Andrén H, Moberg F, Moen J, Bengtsson J. 2013. Higher levels of multiple ecosystem services are found in forests with more tree species. Nat Commun 4:1340.

Gazol A, Camarero JJ. 2016. Functional diversity enhances silver fir growth resilience to an extreme drought. J Ecol 104:1063–75.

Gazol A, Camarero JJ, Anderegg WRL, Vicente-Serrano SM. 2017. Impacts of droughts on the growth resilience of Northern Hemisphere forests. Glob Ecol Biogeogr 26:166–76.

Gazol A, Camarero JJ, Gutiérrez E, Popa I, Andreu-Hayles L, Motta R, Nola P, Ribas M, Sangüesa-Barreda G, Urbinati C, Carrer M. 2015. Distinct effects of climate warming on populations of silver fir (Abies alba) across Europe. J Biogeogr 42:1150–62.

Giuggiola A, Bugmann H, Zingg A, Dobbertin M, Rigling A. 2013. Reduction of stand density increases drought resistance in xeric Scots pine forests. For Ecol Manag 310:827–35. https://doi.org/10.1016/j.foreco.2013.09.030.

Grossiord C. 2018. Having the right neighbors: how tree species diversity modulates drought impacts on forests. New Phytol:0–2. https://doi.org/10.1111/nph.15667

Grossiord C, Granier A, Ratcliffe S, Bouriaud O, Bruelheide H, Checko E, Forrester DI, Dawud SM, Finer L, Pollastrini M, Scherer-Lorenzen M, Valladares F, Bonal D, Gessler A. 2014. Tree diversity does not always improve resistance of forest ecosystems to drought. Proc Natl Acad Sci 111:14812–5. https://doi.org/10.1073/pnas.1411970111

Hargreaves GH, Samani ZA. 1985. Reference crop evapotranspiration from temperature. Appl Eng Agric 1:96–9.

Hartmann H. 2011. Will a 385 million year-struggle for light become a struggle for water and for carbon? How trees may cope with more frequent climate change-type drought events. Glob Chang Biol 17:642–55.

Holmes RL. 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-ring Bull 43:69–78.

Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmidt B, Setala H, Symstad AJ, Vandermeer J, Wardle DA. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol Monogr 75:3–35. https://doi.org/10.1890/04-0922

IPCC. 2018. Chapter 3: Impacts of 1.5°C global warming on natural and human systems. http://www.ipcc.ch/report/sr15/

Jactel H, Gritti ES, Drössler L, Forrester DI, Mason WL, Morin X, Pretzsch H, Castagneyrol B. 2018. Positive biodiversity–productivity relationships in forests: Climate matters. Biol Lett 14:12–15.

Jones HG, Sutherland RA. 1991. Stomatal control of xylem embolism. Plant Cell Environ 14:607–12.

Jourdan M, Kunstler G, Morin X. 2019. How neighbourhood interactions control the temporal stability and resilience to drought of trees in mountain forests. J Ecol.

Jucker T, Avăcăriei D, Bărnoaiea I, Duduman G, Bouriaud O, Coomes DA. 2016. Climate modulates the effects of tree diversity on forest productivity. J Ecol 104:388–98. https://doi.org/10.1111/1365-2745.12522

Jucker T, Bouriaud O, Avacaritei D, Coomes DA. 2014. Stabilizing effects of diversity on aboveground wood production in forest ecosystems: linking patterns and processes. Ecol Lett 17:1560–9. https://doi.org/10.1111/ele.12382

Kolář T, Čermák P, Trnka M, Žid T, Rybníček M. 2017. Temporal changes in the climate sensitivity of Norway spruce and European beech along an elevation gradient in Central Europe. Agric For Meteorol 239:24–33.

Lebourgeois F, Gomez N, Pinto P, Mérian P. 2013. Mixed stands reduce Abies alba tree-ring sensitivity to summer drought in the Vosges mountains, western Europe. For Ecol Manage 303:61–71. https://doi.org/10.1016/j.foreco.2013.04.003.

Leuschner C, Ellenberg H. 2017. Ecology of Central European Forests.

Lévesque M, Rigling A, Bugmann H, Weber P, Brang P. 2014. Growth response of five co-occurring conifers to drought across a wide climatic gradient in Central Europe. Agric For Meteorol 197:1–12. https://doi.org/10.1016/j.agrformet.2014.06.001.

Lévesque M, Saurer M, Siegwolf R, Eilmann B, Brang P, Bugmann H, Rigling A. 2013. Drought response of five conifer species under contrasting water availability suggests high vulnerability of Norway spruce and European larch. Glob Chang Biol 19:3184–99.

Lloret F, Keeling EG, Sala A. 2011. Components of tree resilience: Effects of successive low-growth episodes in old ponderosa pine forests. Oikos 120:1909–20.

Loreau M, Hector A. 2001. Partitioning selection and complementarity in biodiversity experiments. Nature 412:72–6.

Mencuccini M, Martínez-Vilalta J, Vanderklein D, Hamid HA, Korakaki E, Lee S, Michiels B. 2005. Size-mediated ageing reduces vigour in trees. Ecol Lett 8:1183–90.

Mérian P, Lebourgeois F. 2011. Size-mediated climate-growth relationships in temperate forests: A multi-species analysis. For Ecol Manage 261:1382–91.

Metz J, Annighöfer P, Schall P, Zimmermann J, Kahl T, Schulze ED, Ammer C. 2016. Site-adapted admixed tree species reduce drought susceptibility of mature European beech. Glob Chang Biol 22:903–20.

Mina M, Huber MO, Forrester DI, Thürig E, Rohner B. 2018. Multiple factors modulate tree growth complementarity in Central European mixed forests. J Ecol 106:1106–19.

Morin X, Fahse L, de Mazancourt C, Scherer-Lorenzen M, Bugmann H. 2014. Temporal stability in forest productivity increases with tree diversity due to asynchrony in species dynamics. Ecol Lett 17:1526–35.

Moritz S, Bartz-Beielstein T. 2017. imputeTS: Time Series Missing Value Imputation in R. R J 9:207.

Nakagawa S, Schielzeth H. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods Ecol Evol 4:133–42.

Olson ME, Soriano D, Rosell JA, Anfodillo T, Donoghue MJ, Edwards EJ, León-Gómez C, Dawson T, Julio Camarero Martínez J, Castorena M, Echeverría A, Espinosa CI, Fajardo A, Gazol A, Isnard S, Lima RS, Marcati CR, Méndez-Alonzo R. 2018. Plant height and hydraulic vulnerability to drought and cold. Proc Natl Acad Sci U S A 115:7551–6.

Pebesma E. 2018. Simple Features for R: Standardized Support for Spatial Vector Data. R J 10:439.

Pinheiro J., Bates D, DebRoy S, Sarkar D, R Core Team. 2018. nlme: Linear and Nonlinear Mixed Effects Models. https://cran.r-project.org/package=nlme

Pretzsch H. 2013. Facilitation and competition in mixed-species forests analyzed along an ecological gradient. Nov Acta Leopoldina NF 114:159–74.

Pretzsch H, Bielak K, Block J, Bruchwald A, Dieler J, Ehrhart HP, Kohnle U, Nagel J, Spellmann H, Zasada M, Zingg A. 2013a. Productivity of mixed versus pure stands of oak (Quercus petraea (Matt.) Liebl. and Quercus robur L.) and European beech (Fagus sylvatica L.) along an ecological gradient. Eur J For Res 132:263–80.

Pretzsch H, Forrester DI, Bauhus J. 2017. Mixed-Species Forests Ecology and Management. Heidelberg: Springer. https://doi.org/10.1007/978-3-662-54553-9

Pretzsch H, del Río M, Ammer C, Avdagic A, Barbeito I, Bielak K, Brazaitis G, Coll L, Dirnberger G, Drössler L, Fabrika M, Forrester DI, Godvod K, Heym M, Hurt V, Kurylyak V, Löf M, Lombardi F, Matović B, Mohren F, Motta R, den Ouden J, Pach M, Ponette Q, Schütze G, Schweig J, Skrzyszewski J, Sramek V, Sterba H, Stojanović D, Svoboda M, Vanhellemont M, Verheyen K, Wellhausen K, Zlatanov T, Bravo-Oviedo A. 2015. Growth and yield of mixed versus pure stands of Scots pine (Pinus sylvestris L.) and European beech (Fagus sylvatica L.) analysed along a productivity gradient through Europe. Eur J For Res 134:927–47.

Pretzsch H, Rötzer T, Matyssek R, Grams TEE, Häberle KH, Pritsch K, Kerner R, Munch JC. 2014. Mixed Norway spruce (Picea abies [L.] Karst) and European beech (Fagus sylvatica

[L.]) stands under drought: from reaction pattern to mechanism. Trees 28:1305–21.

Pretzsch H, Schütze G, Uhl E. 2013b. Resistance of European tree species to drought stress in mixed versus pure forests: Evidence of stress release by inter-specific facilitation. Plant Biol 15:483–95.

Primicia I, Camarero JJ, Janda P, Čada V, Morrissey RC, Trotsiuk V, Bače R, Teodosiu M, Svoboda M. 2015. Age, competition, disturbance and elevation effects on tree and stand growth response of primary Picea abies forest to climate. For Ecol Manage 354:77–86.

R Core Team. 2019. R: A Language and Environment for Statistical Computing. Vienna, Austria 0. https://www.r-project.org/

Ratcliffe S, Wirth C, Jucker T, van der Plas F, Scherer-Lorenzen M, Verheyen K, Allan E, Benavides R, Bruelheide H, Ohse B, Paquette A, Ampoorter E, Bastias CC, Bauhus J, Bonal D, Bouriaud O, Bussotti F, Carnol M, Castagneyrol B, Chećko E, Dawud SM, De Wandeler H, Domisch T, Finér L, Fischer M, Fotelli M, Gessler A, Granier A, Grossiord C, Guyot V, Haase J, Hättenschwiler S, Jactel H, Jaroszewicz B, Joly FX, Kambach S, Kolb S, Koricheva J, Liebersgesell M, Milligan H, Müller S, Muys B, Nguyen D, Nock C, Pollastrini M, Purschke O, Radoglou K, Raulund-Rasmussen K, Roger F, Ruiz-Benito P, Seidl R, Selvi F, Seiferling I, Stenlid J, Valladares F, Vesterdal L, Baeten L. 2017. Biodiversity and ecosystem functioning relations in European forests depend on environmental context. Ecol Lett 20:1414–26.

Rigling A, Moser B, Feichtinger L, Gärtner H, Giuggiola A, Hug C, Wohlgemuth T. 2018. 20 Jahre Waldföhrensterben im Wallis: Rückblick und aktuelle Resultate. Schweizerische Zeitschrift fur Forstwes 169:242–50. https://doi.org/10.3188/szf.2018.0242

Rohner B, Weber P, Thürig E. 2016. Bridging tree rings and forest inventories: How climate effects on spruce and beech growth aggregate over time. For Ecol Manage 360:159–69.

Rötzer T, Häberle KH, Kallenbach C, Matyssek R, Schütze G, Pretzsch H. 2017. Tree species and size drive water consumption of beech/spruce forests - a simulation study highlighting growth under water limitation. Plant Soil 418:337–56.

Rozas V, DeSoto L, Olano JM. 2009. Blackwell Publishing Ltd Sex-specific, age-dependent sensitivity of tree-ring growth to climate in the dioecious tree Juniperus thurifera. New Phytol 182:687–97.

Sánchez-Salguero R, Camarero JJ, Carrer M, Gutiérrez E, Alla AQ, Andreu-Hayles L, Hevia A, Koutavas A, Martínez-Sancho E, Nola P, Papadopoulos A, Pasho E, Toromani E, Carreira JA, Linares JC. 2017. Climate extremes and predicted warming threaten Mediterranean Holocene firs forests refugia. Proc Natl Acad Sci U S A 114:E10142–50.

Schäfer C, Grams TEE, Rötzer T, Feldermann A, Pretzsch H. 2017. Drought stress reaction of growth and $\delta$13C in tree rings of European beech and Norway spruce in monospecific versus mixed stands along a precipitation gradient. Forests 8:177.

Schuler LJ, Bugmann H, Snell RS. 2017. From monocultures to mixed-species forests: is tree diversity key for providing ecosystem services at the landscape scale? Landsc Ecol 32:1499–516.

Schwarz JA, Bauhus J. 2019. Benefits of Mixtures on Growth Performance of Silver Fir (Abies alba) and European Beech (Fagus sylvatica) Increase With Tree Size Without Reducing Drought Tolerance.

Shannon CE, Weaver W. 1948. A Mathematical Theory of Communication. Bell Syst Tech J 27:623–56.

Sohn JA, Saha S, Bauhus J. 2016. Potential of forest thinning to mitigate drought stress: A meta-analysis. For Ecol Manage 380:261–73. https://doi.org/10.1016/j.foreco.2016.07.046.

Speer JH. 2009. Fundamentals of tree-ring research.

Spinoni J, Vogt JV, Naumann G, Barbosa P, Dosio A. 2018. Will drought events become more frequent and severe in Europe? Int J Climatol 38:1718–36.

Stokes A, Norris JE. 2007. Eco-and Ground Bio-Engineering: The Use of Vegetation to Improve Slope Stability.

Teets A, Fraver S, Weiskittel AR, Hollinger DY. 2018. Quantifying climate–growth relationships at the stand level in a mature mixed-species conifer forest. Glob Chang Biol.

Thornton PE, Running SW, White MA. 1997. Generating surfaces of daily meteorological variables over large regions of complex terrain. J Hydrol 190:214–51.

Thurm EA, Uhl E, Pretzsch H. 2016. Mixture reduces climate sensitivity of Douglas-fir stem growth. For Ecol Manage 376:205–20. https://doi.org/10.1016/j.foreco.2016.06.020.

Tinner W, Colombaroli D, Heiri O, Henne PD, Steinacher M, Untenecker J, Vescovi E, Allen JRM, Carraro G, Conedera M, Joos F, Lotter AF, Luterbacher J, Samartin S, Valsecchi V. 2013. The past ecology of *Abies alba* provides new perspectives on future responses of silver fir forests to global warming. Ecol Monogr 83:419–39.

Tobner CM, Paquette A, Gravel D, Reich PB, Williams LJ, Messier C. 2016. Functional identity is the main driver of diversity effects in young tree communities. Ecol Lett 19:638–47.

Toïgo M, Vallet P, Perot T, Bontemps JD, Piedallu C, Courbaud B. 2015. Overyielding in mixed forests decreases with site productivity. J Ecol 103:502–12.

Trenberth KE, Dai A, Van Der Schrier G, Jones PD, Barichivich J, Briffa KR, Sheffield J. 2014. Global warming and changes in drought. Nat Clim Chang 4:17–22.

Vanhellemont M, Sousa-Silva R, Maes SL, Van den Bulcke J, Hertzog L, De Groote SRE, Van Acker J, Bonte D, Martel A, Lens L, Verheyen K. 2019. Distinct growth responses to drought for oak and beech in temperate mixed forests. Sci Total Environ 650:3017–26. https://www.sciencedirect.com/science/article/pii/S0048969718339275?via%3Dihub

Vicente-Serrano SM, Beguería S, López-Moreno JI. 2010. A multiscalar drought index sensitive to global warming: The standardized precipitation evapotranspiration index. J Clim 23:1696–718.

Vilà M, Carrillo-Gavilán A, Vayreda J, Bugmann H, Fridman J, Grodzki W, Haase J, Kunstler G, Schelhaas MJ, Trasobares A. 2013. Disentangling Biodiversity and Climatic Determinants of Wood Production. PLoS One 8.

Vitali V, Büntgen U, Bauhus J. 2017. Silver fir and Douglas fir are more tolerant to extreme droughts than Norway spruce in south-western Germany. Glob Chang Biol 23:5108–19.

Vitali V, Forrester DI, Bauhus J. 2018. Know Your Neighbours: Drought Response of Norway Spruce, Silver Fir and Douglas Fir in Mixed Forests Depends on Species Identity and Diversity of Tree Neighbourhoods. Ecosystems 21:1215–29.

Vitasse Y, Bottero A, Cailleret M, Bigler C, Fonti P, Gessler A, Lévesque M, Rohner B, Weber P, Rigling A, Wohlgemuth T. 2019a. Contrasting resistance and resilience to extreme drought and late spring frost in five major European tree species. Glob Chang Biol 25:3781–92.

Vitasse Y, Bottero A, Rebetez M, Conedera M, Augustin S, Brang P, Tinner W. 2019b. What is the potential of silver fir to thrive under warmer and drier climate? Eur J For Res. https://doi.org/10.1007/s10342-019-01192-4.

Weber P, Bugmann H, Fonti P, Rigling A. 2008. Using a retrospective dynamic competition index to reconstruct forest succession. For Ecol Manage 254:96–106.

Yachi S, Loreau ML. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. Proc Natl Acad Sci 96:1463–8.

Yoder BJ, Ryan MG, Waring RH, Schoettle AW, Kaufmann MR. 1994. Evidence of reduced photosynthetic rates in old trees. For Sci.

Zang C, Biondi F. 2015. Treeclim: An R package for the numerical calibration of proxy-climate relationships. Ecography (Cop) 38:431–6.

Zang C, Hartl-Meier C, Dittmar C, Rothe A, Menzel A. 2014. Patterns of drought tolerance in major European temperate forest trees: Climatic drivers and levels of variability. Glob Chang Biol 20:3767–79.

Zuur AF, Ieno EN, Walker NJ, A. SA, Smith GM. (2009). Mixed Effects Models and Extensions in Ecology with R. Springer Science & Business Media. http://arxiv.org/abs/1305.6995